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Microtus townsendii.

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Microtus townsendii (Bachman, 1839)

Townsend's Vole

Arvicola townsendii Bachman, 1839:60. Type locality "Columbia River"; lower Columbia River near mouth of the Willamette River on or near Wappatoo (or Sauvie) Island, Oregon (Bailey, 1900).

Arvicola occidentalis Peale, 1848:45. Type locality "Puget Sound, Oregon" [Washington].

Arvicola tetramerus Rhoads, 1894:283. Type locality "Beacon Hill Park, Vancouver Island, British Columbia."

M[icrotus]. townsendii: Miller, 1896:66. First use of name combination.

CONTEXT AND CONTENT. Order Rodentia, Family Muridae, Subfamily Arvicolinae, Genus *Microtus*, Subgenus *Microtus* (Carleton and Musser, 1984; Hall, 1981; Hooper and Hart, 1962). Six subspecies are recognized currently as follows (Hall, 1981):

M. t. cowani Guiguet, 1955:B67. Type locality "Triangle Island, B[ritish]. C[olumbia]., 129°05′ west, 50°55′ north."

M. t. cummingi Hall, 1936:15. Type locality "Bowen Island, Howe Sound, British Columbia."

M. t. laingi Anderson and Rand, 1943:74. Type locality "Port Hardy, North Vancouver Island," British Columbia.

M. t. pugeti Dalquest, 1940:7. Type locality "Neck Point, northwest corner of Shaw Island, San Juan County, Washington."

M. t. tetramerus (Rhoads, 1894:283), see above.

M. t. townsendii (Bachman, 1839:60), see above.

DIAGNOSIS. *Microtus townsendii* is a large dark-brownish vole with large broad ears that extend above the fur; tail long, usually blackish or brownish; feet brownish or blackish with brown claws (Bachman, 1839; Bailey, 1900). The skull (Fig. 1) is long, angular, and heavily ridged in older specimens; incisive foramina long, narrow, and constricted posteriorly; palate with deep lateral pits (Bailey, 1900).

Microtus townsendii (Fig. 2) can be distinguished from sympatric congeners by the following characters: from *M. oregoni* by eye >4 mm in diameter, four loops of enamel on lingual side of M3, and a longer tail; from *M. canicaudus* by nearly uniformly blackish or dark-brownish tail, U-shaped margin of palate, and incisive foramina >6 mm long; from *M. richardsoni* by six plantar tubercles, incisive foramina not forming narrow slits posteriorly, and incisors not greatly procumbent; from *M. californicus* by nearly uniformly blackish or dark-brownish tail, incisive foramina widest in the anterior half, and incisors not entirely obscured by nasals in dorsal view; from *M. longicaudus* by nearly uniformly blackish or dark-brownish tail, tail <50% of head and body length, and incisors not entirely obscured by nasals in dorsal view; from *M. pennsylvanicus* by M2 with four loop of enamel and tail >30% of head and body length. Distinguishing characteristics were adapted from Dalquest (1948), Hall (1981), Ingles (1965), and Verts and Carraway (1984).

GENERAL CHARACTERS. Townsend's vole is one of the largest voles in North America (Hall, 1981). Ranges in external measurements (in mm) of *M. townsendii* (Hall, 1981; Hall and Cockrum, 1953) are: total length, 169 to 225; tail length, 48 to 70; length of hind foot, 20 to 26; ear length, 15 to 17. With few exceptions, these extremes are not exceeded by measurements provided by Bailey (1900, 1936), Banfield (1974), Dalquest (1940, 1948), Maser and Storm (1970), and Rhoads (1894). Means and extremes (in parentheses) of measurements (in mm) of eight adults of the largest subspecies, *M. t. cowani* (Cowan and Guiguet, 1956) are: total length, 220 (202 to 235); tail length, 70 (61 to 75); length of hind foot, 28 (27 to 29). The body is 2.2 to 2.4 times as long as the tail and the tail is 2.2 to 2.6 times as long as the hind foot (Hall, 1981). Body mass of adult *M. townsendii* ranges from 47 to 82.5 g (Maser and Storm, 1970). Pearson (1972) reported significant differences in mass between males ($\bar{X} = 64.0$ g, $n = 7$) and females ($\bar{X} = 51.8$ g, $n = 4$).

The auditory bullae are medium sized and well rounded (Bailey, 1900). Means and extremes (in parentheses) of selected skull measurements (in mm) from eight adult *M. t. pugeti* (Dalquest, 1940) are: basal length, 28.4 (27.3 to 29.8); zygomatic breadth, 17.1 (16.4 to 17.8); length of nasals, 3.4 (3.2 to 3.7); greatest combined width of nasals, 8.3 (7.9 to 8.5); greatest width of rostrum, 5.6 (5.4 to 6.0); alveolar length of molar toothrow, 7.4 (7.0 to 7.8); least interorbital breadth, 4.0 (3.8 to 4.2). Average skull measurements (in mm) for six adult *M. t. tetramerus* (Rhoads, 1894) are: total length of skull, 26.5; basilar length, 24.0; zygomatic breadth, 15.0; length of nasals, 7.5; incisors to postpalatal notch, 14.2; interorbital constriction, 3.4; length of mandible, 16.0; width of mandible, 8.5.

The dentition is heavy; m2 has four closed triangles and a posterior loop, m3 has an anterior crescent, three closed triangles, and a posterior loop, and M1 has five closed triangles (Bailey, 1900). The dental formula is i 1/1, c 0/0, p 0/0, m 3/3, total 16.

The fur is thin and harsh with the ears extending conspicuously above the fur (Bailey, 1900, 1936). The upper parts are dark brownish with a heavy mixture of black-tipped guard hairs; the tail is slightly bicolored, blackish above (Hall, 1981); feet are lead colored (Bailey, 1900). Young are darker than adults and have a dusky belly, and blackish feet and tail (Bailey, 1900).

DISTRIBUTION. The geographic range of *M. townsendii* (Fig. 3) extends from Triangle Island, British Columbia, south to Humboldt Bay, California, and east in British Columbia to Chilliwack; in Washington to Sauk, Nisqually Flats, and Clark Co.; in Oregon to Salem, Eugene, and Prospect (Hall, 1981). Altitudinally, Townsend's voles range from sea level to about 1,830 m (Johnson and Johnson, 1952; Maser and Storm, 1970) in the Olympic Mountains, Washington. They also occur to about 914 m in the Cascade Mountains, Oregon (Howell, 1920).

Microtus t. cowani is known only from Triangle Island, British Columbia (Guiguet, 1955). *M. t. cummingi* has been found only on Bowen and Texada islands, British Columbia (Cowan and Guiguet, 1956). The range of *M. t. laingi* includes Vancouver Island, British Columbia, from Cape Scott south to Sayward, and to Beaver Creek near Alberni (Cowan and Guiguet, 1956). It also occurs on Hope, Hurst, and Nigei islands (Cowan and Guiguet, 1956). *M. t. pugeti* only occurs on Shaw, San Juan, and Cypress islands, San Juan Co., Washington (Dalquest, 1940). *M. t. tetramerus* is found on Vancouver Island, British Columbia, from Victoria to Comox on the east coast and on the west coast to Alberni (Cowan and Guiguet, 1956). It also occurs on a small island 3.3 km NE of Tofino, and on Saltspring, Vargas, Pender, and Bunsby islands in British Columbia (Cowan and Guiguet, 1956). *M. t. townsendii* occurs in southwestern British Columbia from Hope to Vancouver, with records from Chilliwack in the east and Port Moody and Lulu Island in the west (Cowan and Guiguet, 1956). Its range continues south through western Washington and Oregon into northern California as far as Eureka (Hall, 1981). The subspecies has not been determined for a population of *M. townsendii* recently reported on Ozette Island, Washington (Aubry and West, 1987). There is no fossil record for *M. townsendii* (E. Anderson, per. comm.).

FORM AND FUNCTION. The fine structure of spermatozoa from *M. townsendii* and *Clethrionomys rutilus* is not significantly different (Koehler, 1978). The general shape of the sperm head is a flattened ellipsoid with a prominent acrosomal hook. Microtubule-like elements (20 to 24 μm in diameter) form a parallel

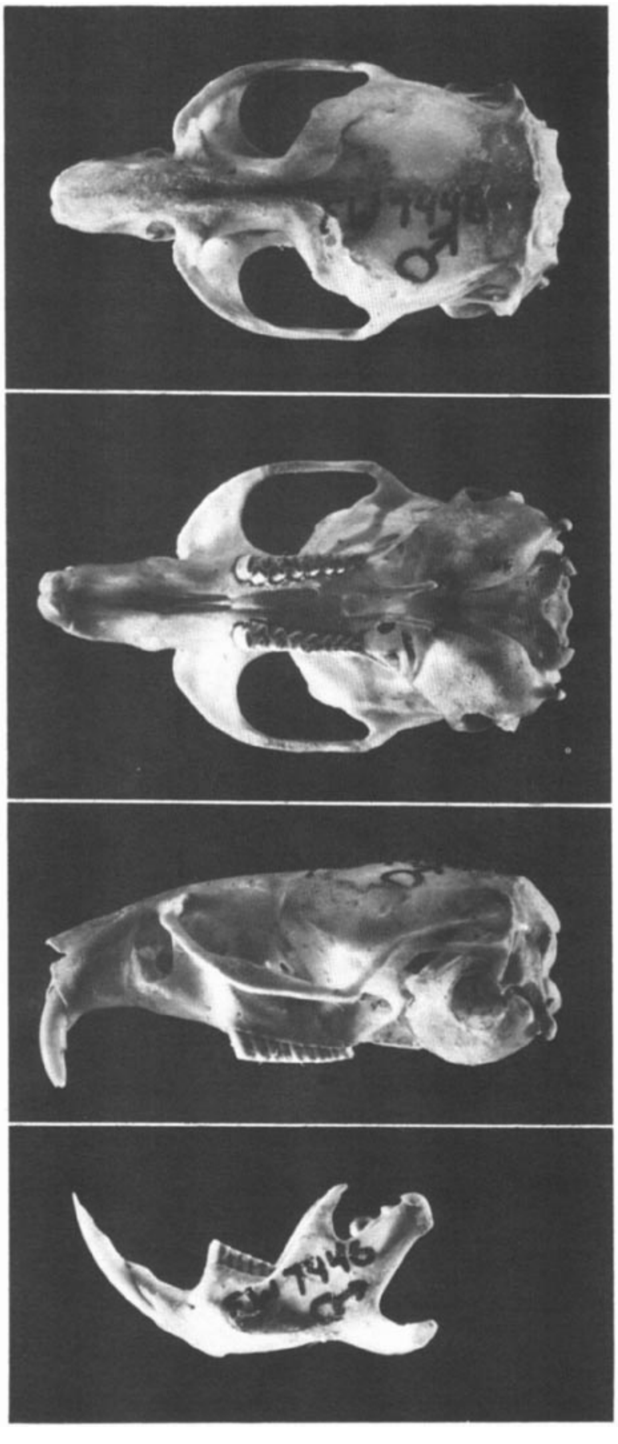

FIG. 1. Dorsal, ventral, and lateral views of cranium, and lateral view of the mandible of male *Microtus townsendii* (Oregon State University, Department of Fisheries and Wildlife mammal collection 7446 from 10½ mi. S, 1 mi W Corvallis, Benton, Co., Oregon). Occipitonasal length of skull is 29.34 mm.

FIG. 2. Photograph of male *Microtus townsendii* from 9 mi N, 3 mi E Corvallis, Benton Co., Oregon.

sheath radiating from the posterior ring to the inferior acrosomal margin just beneath the plasma membrane (Koehler, 1978). Fine filaments (5 to 8 μm in diameter) are associated with the cell surface, especially in the region of concave curvature of the acrosomal hook. Koehler (1978) suggested that these structures may serve cytoskeletal roles aiding stabilization of the respective areas and in maintenance of the shape of the mature sperm head.

In general, the glans penis of *Microtus* is rather barrel-like, with a shallow middorsal trough and a midventral raphe (Hooper and Hart, 1962). The rim of the barrel is divisible into three structural areas: a dorsal lobe and two ventrolateral sectors. The glans penis of three specimens of *M. townsendii* averaged 5.4 mm in length and 3.5 mm in diameter (Hooper and Hart, 1962). The dorsal lobe has one or two papillae on the outer edge of each peak and each ventrolateral sector has six to nine fingers of different lengths. *Microtus townsendii*, *M. pennsylvanicus*, and *M. montanus* have penes similar in overall external contour, dorsal papilla, and numbers of rim papillae (Hooper and Hart, 1962), but *M. townsendii* has more papillose dorsal lobes, more fingers on dorsolateral sectors of the rim, and larger spinose areas on crater walls and floor than *M. montanus*.

The urethral process on the penis of *M. townsendii* consisted of two large lateral arms that curve to the side, and a medial lobe split distally (Hooper and Hart, 1962). In *M. townsendii* and *M. montanus*, the medial lobe of the urethral process is as long as the hooked lateral arms, but in *M. pennsylvanicus* the medial lobe is short.

The baculum (Fig. 4) in microtines consists of an elongate stalk, having a laterally, and, to a lesser extent, dorsoventrally expanded base and an attenuate distal shaft (Anderson, 1960). The baculum has a broad stalk about 3.0 mm long with a round tip and three well-developed ossified processes (Anderson, 1960). The median process is >40% of the length of the stalk, straight, and more than twice as large as the dorsally curved lateral processes (Anderson, 1960). Mean measurements (in mm) for bacula from three *M. townsendii* (Hooper and Hart, 1962) are: total length, 4.7; length of proximal bone, 3.1; length of medial rod, 1.6; length of medial ossicle, 1.3; length of lateral ossicle, 0.9. The base is broad with well-developed, medially confluent tuberosities (Anderson, 1960) and usually comes to a wide triangular point proximally (Hooper and Hart, 1962). The shape of the proximal bone of the baculum is similar in *M. townsendii*, *M. montanus*, and *M. pennsylvanicus*. The digits of the baculum are less ossified in *M. townsendii* and *M. montanus* than in *M. pennsylvanicus*.

Male *M. townsendii* have conspicuous hip glands (Bailey, 1900). Quay (1968) noted that the largest males had the most developed glands. MacIsaac (1977) found that 56% of nonbreeding female *M. townsendii* and 91% of breeding females had recognizable hip glands. The length of the glands is highly correlated with reproductive condition in both males and females with breeding voles having larger hip glands (MacIsaac, 1977). MacIsaac (1977) reported that development of hip glands in *M. townsendii* was under androgen control. According to Quay (1954) *M. townsendii* has five meiboian glands on the dorsal eyelid, but none on the ventral eyelid.

Carleton (1981) reported that the stomach of *M. townsendii* has a deep incisura angularis, and emarginate bordering fold with processes concentrated on the left rim of the fold, and an intermediate grade III glandular zone. All species of *Microtus* that Carleton (1981) examined had uniform stomach morphology.

Water consumption by 13 *M. townsendii* averaged 0.53 cc g^{-1} day^{-1} (Pearson, 1972). Males ($n = 7$) averaged 0.48 cc g^{-1} day^{-1} and females ($n = 6$) consumed 0.59 cc g^{-1} day^{-1}. There were no significant differences between rates of water consumption of males and females. Food intake for four individuals averaged 0.13 g g^{-1} day^{-1}.

Female *M. townsendii* have 7 to 12 times the total and free corticosterone concentrations in their plasma as males (McDonald and Taitt, 1982). Males over 80 g had concentrations of plasma androgens to 4 times those of smaller males. Castration had no effect on total concentration of corticosterone or corticosteroid-binding globulin in the plasma of males.

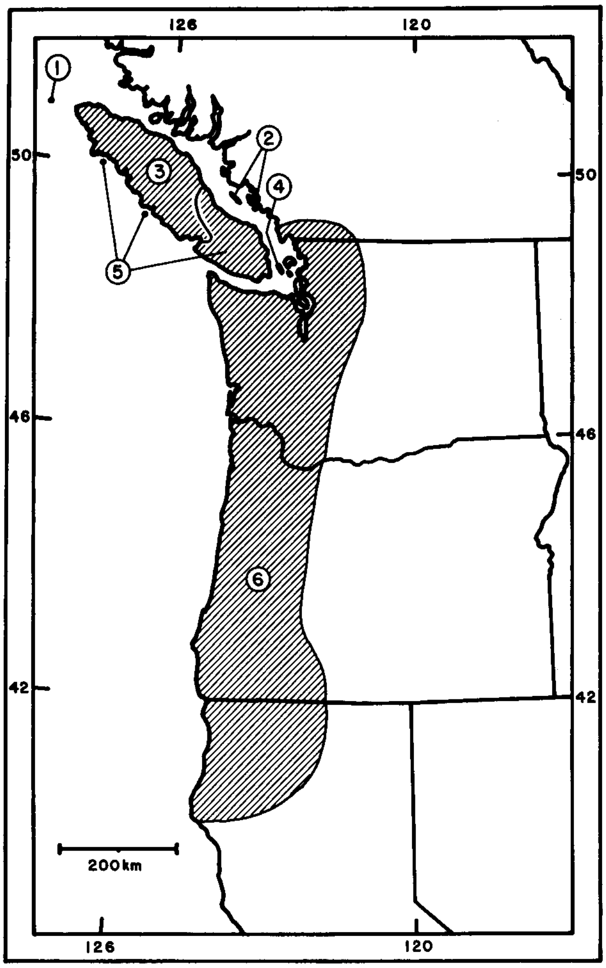

FIG. 3. Distribution of *Microtus townsendii*. Subspecies are: 1, *M. t. cowani*; 2, *M. t. cummingi*; 3, *M. t. laingi*; 4, *M. t. pugeti*; 5, *M. t. tetramerus*; 6, *M. t. townsendii*. Map redrawn after Hall (1981).

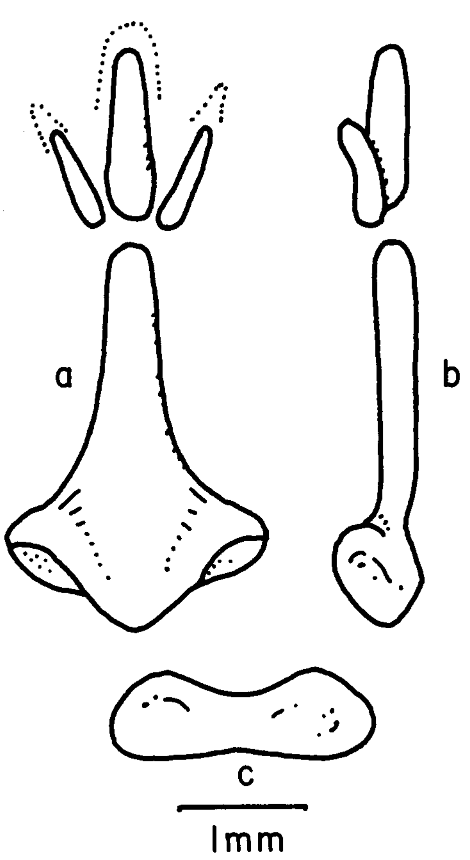

FIG. 4. Dorsal (a), right lateral (b), and proximal (c; dorsum upward) views of baculum of *Microtus townsendii*. Redrawn after Anderson (1960).

ONTOGENY AND REPRODUCTION. In the laboratory, 16 of 20 female *M. townsendii* had perforate vaginae by 54 days of age, but vaginae of the three youngest (18 to 20 days) and smallest (39 to 41 g) females closed for 5 to 17 days after being perforate for 2 to 5 days. Age and body mass of females at first estrus ranged from 35 to 80 days and 36 to 48 g, respectively; puberty was correlated more closely with body mass than with age (MacFarlane and Taylor, 1981). In the field, females <15 g had imperforate vaginae, but perforation occurred in most females before they weighed 45 g. First estrus was detected at 18.5 g in most wild females, half the weight of laboratory-raised females. Body mass at which females attained sexual maturity in the field was related directly to the density of adult females, but not to that of adult males (Boonstra, 1978). Although MacFarlane and Taylor (1981) were aware that LeDuc and Krebs (1975) reported differences in body mass at puberty in the wild as much as 36 g, they suggested that isolation from males might be responsible for greater average body mass of females at puberty in the laboratory. Of seven 16- to 21-g wild females, all but the lightest individual exhibited follicular development; the heaviest had mated and ovulated, and possessed corpora lutea and five two-celled zygotes (MacFarlane and Taylor, 1981). MacFarlane and Taylor (1981) concluded that sterile breeding cycles were not significant in *M. townsendii* and that fruitful matings could occur at first or second estrus. During spring and summer, males >30 g usually were sexually mature (MacFarlane and Taylor, 1982*a*).

Vaginal smears at 24-h intervals on 12 isolated adult females revealed stages similar to those reported for *Mus musculus*, ". . . although stages other than estrus are not as clearly defined" (MacFarlane and Taylor, 1982*b*:104). Duration of estrus averaged 4.5 days (range, 1 to 19 days) with cornified epithelium the primary cell type present; diestrus lasted an average of 3.2 days (range, 1 to 18 days) and was described as either "light" with primarily acellular smears or "heavy" with smears containing mostly mucous with many leucocytes (MacFarlane and Taylor, 1982*b*). Diestrus preceded and followed estrus in 65% and 69% of the instances, respectively; metestrus preceded estrus and followed estrus in 14% and 30%, respectively; and proestrus preceded estrus in 21% and followed estrus in one instance (MacFarlane and Taylor, 1982*b*). Intervals between successive estrus periods averaged 8 days (range, 2 to 28 days); because 70% of the intervals were <8 days and the variability was considerable, MacFarlane and Taylor (1982*b*) believed that regular cycles in *M. townsendii* were not detected by their studies of vaginal smears. Detailed examination of the histology of oviducts, vaginae, and uterine horns during various stages of the cycle suggested that failure to detect the regular sequence of the estrus cycle by vaginal smears might be related largely to sampling at intervals >24 h. Administration of 25 or 50 I.U. of Wellcome's pregnant mare's serum gonadatrophin induced perforation of vaginae in eight of nine females, but did not induce ovulation. Because of absence of evidence of ovulation, corpora lutea, and corpora albicantia in ovaries of the 12 adult females examined and in 9 females to which pregnant mare's serum was administered, and presence of spermatozoa in vaginae or oviducts of females that had ovulated recently, MacFarlane and Taylor (1982*b*) suggested that *M. townsendii* was an induced ovulator, an attribute reported for several other *Microtus*.

Means and ranges (in parentheses) of maximum diameters of ovaries (in mm) and maximum diameters of follicles (in μm), respectively, during various stages of the estrus cycle (MacFarlane and Taylor, 1982*b*) were: anestrus (n = 10), 1.22 (0.96 to 1.37), 394.5 (285 to 435); diestrus (n = 9), 1.33 (1.15 to 1.55), 404 (360 to 473); estrus (n = 9), 1.55 (1.44 to 1.79), 479 (398 to 585); metestrus (n = 2), 1.63 (1.57 to 1.68), 480 (450 to 510). Mean cross-sectional diameters (in mm) of uterine horns were 0.58, 0.76, and 1.20 for anestrous, diestrous, and estrous females, respectively.

The length of the breeding season in *M. townsendii*, as in several other microtines, is related to the stage in the multiannual cycle of abundance (Beacham, 1980*a*). On Reifel Island, British Columbia, Beacham (1980*a*) found the Townsend's vole in breeding condition from 10 May (when studies commenced) to October in 1976, from early February (50% of both sexes were in breeding condition by late February) to mid-August in 1977, and from mid-February (over 50% breeding by mid-March) to May 1978 (when studies ceased). The early cessation of breeding in 1977 when the density peaked, was attributed to selective dispersal or death of sexually mature voles that overwintered from 1976 and failure of young voles born early in the year to mature sexually during summer (Beacham, 1980*a*).

Gestation periods of 21, 23 and 24 days were recorded for three females in captivity; the latter female was nursing a litter of five during a postpartum pregnancy (MacFarlane and Taylor, 1982*a*). Mean litter size was reported to be four (range one to nine) in British Columbia (Cowan and Guiguet, 1956) and seven (range five to eight) in Washington (Dalquest, 1948); in Oregon, the range was reported as two to 10 (Maser et al., 1981). In British Columbia, MacFarlane and Taylor (1982*a*) found females that conceived in the laboratory ($n = 13$) gave birth to a mean of 4.8 (range two to six) young, whereas females bred in the field that gave birth in the laboratory within 5 days of capture ($n = 12$) produced an average of 5.4 (range two to seven) offspring; mean number of embryos per pregnant female ($n = 20$) was 6.0 (range five to seven). On Westham Island, British Columbia, mean ($\pm SE$) numbers of embryos per pregnant female were 4.96 ± 1.19 in fall of 1973 ($n = 66$), 5.42 ± 1.12 in spring 1974 ($n = 92$), and 4.92 ± 1.00 in summer 1974 ($n = 120$); mean numbers of embryos were significantly different between seasons (Anderson and Boonstra, 1979). Also, mean numbers of embryos were not related to parity of females, but, in both samples collected in 1974, numbers of embryos were correlated significantly with body mass of mothers (Anderson and Boonstra, 1979). Based on a theoretical maximum detectable rate of pregnancy of 71% (as pregnancy could be detected only during the last 15 days of gestation) if all females were pregnant continuously, Anderson and Boonstra (1979) estimated rates of pregnancy to range from 0 to 70.6%; breeding seemed to cease during winter.

Pregnancy success, based on the proportion of obviously pregnant females lactating 2 weeks later, was 46.4% in 455 pregnant females examined in British Columbia; success was correlated positively ($P < 0.05$) with population growth (Boonstra, 1980). Thus, infanticide and blockage of pregnancy (Bruce effect) were rejected as possible causes of declines from peak densities. Reproductive success, measured in terms of one or more offspring of detectably pregnant females entering traps, was 59% in 6- by 6-m enclosures each containing one adult male and one adult female, a rate considered to underestimate prenatal and postpartum losses (Anderson and Boonstra, 1979). Of 44 unsuccessful pregnancies, 68.2% of the litters were lost during late pregnancy or at parturition. Litters born in traps were nearly always unsuccessful. Recruitment was highest in spring and autumn, lowest in summer and winter (Anderson and Boonstra, 1979); recruitment also was an inverse function of the density of females, but not of males (Redfield et al., 1978).

In captivity, weaning of offspring occurred at 15 to 17 days of age, although young were observed to consume both food and water several days earlier (MacFarlane, 1977). Twenty females averaged 15.1 g (range 11.4 to 20.0) at weaning. From our interpretation of data presented graphically, body mass of the 20 females averaged about 29 g at 25 days of age, 37 g at 35 days, 40 g at 45 days, and 42 g at 55 days (MacFarlane, 1977). Relative growth rates (body mass/body mass predicted from second-degree polynomial regression) of wild males <50 g differed by season (greatest in autumn, less in summer, least in spring) and was related inversely to the density of adult males (Boonstra, 1978). Beacham (1980*e*) reported that male *M. townsendii* always grew faster than females, that growth patterns varied by season, by size of the vole, and by age.

Korn and Taitt (1987) supplied a population of *M. townsendii* with rolled oats containing 40 μg/g 6-methoxybenzoxazolinone (6-MBOA). Females matured at a lower body mass and attained breeding condition 4 weeks earlier than females in a control population; also, young were recruited and attained reproductive competence themselves 4 weeks earlier in the treated population. However, among males, 6-MBOA did not seem to produce ". . . a direct positive effect on reproduction," thus, males and females may ". . . respond to different cuing mechanisms for the initiation of breeding" (Korn and Taitt, 1987:595–596). Early maturity of females can enhance population growth, thus, Korn and Taitt (1987:596) postulated that with 6-MBOA it might be possible to ". . . create out-of-phase cyclic populations . . . [and, thereby] . . . differentiate between extrinsic and intrinsic population processes."

ECOLOGY. Dalquest (1940, 1948) reported that the two races of *M. townsendii* found in Washington occur only in the humid subdivision of the Transition life zone. The subspecies *M. t. townsendii* lives in marshes or damp meadows, under cover of deep, rank vegetation. These voles avoid forested areas and dry brush, but sometimes occur in dry grass. Voles of the race *M. t. pugeti* occur in meadows, salt marshes, driftwood strewn on sea beaches, piles of rocks, and areas of sparse, dry grass. *M. townsendii* has been captured in forest habitats on San Juan Island (Dalquest, 1940) and Ozette Island (Aubry and West, 1987), Washington.

In British Columbia, *M. townsendii* is found in moist fields and sedge (*Carex* sp.) meadows of the alluvial areas of the Fraser River delta and similar habitats on Vancouver Island (Cowan and Guiguet, 1956). It also is found to timberline and above in the alpine and subalpine meadows on Vancouver Island and in dense, lush vegetation on certain islands used as rookeries by seabirds (Cowan and Guiguet, 1956).

Along the Oregon coast, *M. townsendii* primarily occupies deflation plains, willow (*Salix* sp.)-sedge marshes, wet pasturelands, and tidal river habitats, but occasionally is found in riparian-alder (*Alnus* sp.) small-stream habitats when sufficient grass meadow occurs adjacent thereto (Maser et al., 1981). Bailey (1936) characterized *M. townsendii* as a marsh or meadow dweller, occurring mostly on wet ground with a dense cover of grass and tules (*Scirpus* sp.). Goertz (1964) called *M. townsendii* chiefly riparian in the Willamette Valley, Oregon, but considered it to occupy moist meadows or irrigated fields that contain dense stands of sedges, bracken fern (*Pteridium aquililinum*), and wild rye (*Elymus* sp.).

In some instances, Maser and Storm (1970) found Townsend's vole in the Willamette Valley in moist, rank meadows at considerable distances from permanent water. In most instances, *M. townsendii* occurs in dense grass and sedge, regardless of the elevation (Goertz, 1964). Howell (1923) considered Townsend's voles to be marsh and meadow bottom dwellers, but reported taking specimens in brush on the Oregon coast far from fields or boggy land.

In California, Elliot (1903) reported that E. Heller collected specimens well out on salt marshes in Humboldt Bay. He quoted from Heller's field notes (p. 189) that voles were "common above tidewater, with habits very similar to those of a muskrat."

The runways of Townsend's voles apparently are used by successive generations and often are worn 2.5 to 5 cm deep (Dalquest, 1948; Maser and Storm, 1970; Maser et al., 1981). These voles keep to their runways in autumn, winter, and spring, but may abandon them when vegetation is dense enough for total concealment (Dalquest, 1948).

At least during wet periods, *M. townsendii* nests on or above the soil surface (Maser and Storm, 1970; Maser et al., 1981), often on hummocks. This habit of nesting above the ground may allow *M. townsendii* to live in seasonally flooded habitats that exclude other species (Hawes, 1975). In the Willamette Valley, Oregon, *M. townsendii* lives in flooded areas most of the winter (Maser and Storm, 1970), even in some areas flooded most of the year where entrances to burrows are under water (Maser et al., 1981). During drier periods, these voles maintain subterranean burrow systems and underground nests. Both summer and winter nests are made with grasses (Maser and Storm, 1970). Dalquest (1948) found only below-ground nests of *M. townsendii* near Seattle, but did not mention the time of year or water conditions.

Droppings frequently are found in runways used by these voles; latrines with heaps of droppings tend to become established at runway intersections. After repeated depositions, latrines reportedly reach 18 cm in length, 8 cm in width, and form a ramp up to 13 cm high (Maser and Storm, 1970).

Townsend's voles eat a variety of tender grassland and marsh vegetation including rushes (*Juncus* sp.), tules, horsetail (*Equisetum arvense*), clover (*Trifolium* sp.), alfalfa (*Medicago sativa*), blue-eyed grass (*Sisyrichium sarmentosum*), purple-eyed grass (*S. bellum*), sedges, velvet grass (*Holcus lanatus*), and other grasses (Bailey, 1936; Dalquest, 1948; Goertz, 1964; Maser and Storm, 1970).

Couch (1925) reported that *M. townsendii* near Olympia, Washington, stored quantities of small bulbous roots of a mint (*Mentha canadensis*). As much as 13.2 l or more of these bulbs were found in single caches. Although green, succulent food was available in abundance during winter, the voles stored and ate the bulbs.

Dalquest (1940) reported that stomachs of certain specimens of *M. t. pugeti* contained masses of rank-smelling, bright green vegetation but others were filled with a starchy, transparent white substance with an onionlike odor. At high elevations on Vancouver Island some whiteheath (*Cassiope mertensiana*) is taken by Townsend's voles (Cowan and Guiguet, 1956). On Texada Island, British Columbia, Townsend's voles injured coniferous trees by removing bark and cambium from stems, branches, and roots (Harper and Harestad, 1986). However, damage was apparently not severe enough to reduce growth of the trees.

Boonstra (1977*a*) attached metal ear tags to most of the *M. townsendii* on three grids on an island near Vancouver, British Columbia, then searched for the tags in raptor pellets and fecal droppings of carnivorous mammals. No attempt was made to distinguish between pellets or droppings of different species, but predators observed in the area included short-eared owls (*Asio flammeus*), great-horned owls (*Bubo virginianus*), snowy owls (*Nyctea scandia*), barn owls (*Tyto alba*), northern harriers (*Circus cyaneus*), rough-legged hawks (*Buteo lagopus*), red-tailed hawks (*Buteo jamaicensis*), northern shrikes (*Lanius excubitor*), great blue herons (*Ardea herodius*), raccoons (*Procyon lotor*), and feral cats (*Felis catus*). Remains of *M. townsendii* were much more abundant than other prey in the pellets and droppings. Of Townsend's voles that disappeared from the grids, 5.9% of their ear tags were recovered from pellets or droppings from December 1972 to April 1973, 30.3% from October 1973 to 10 December 1973, and 19.0% from 22 December 1973 through April 1974. Boonstra (1977*a*) estimated that predation accounted for <8% of the loss of tagged animals during the winter-spring decline in 1972–1973 and <20% during 1973–1974. Therefore, he concluded that predation was not necessary to initiate or maintain a decline in numbers of voles.

In a similar study on a nearby island, Beacham (1979*a*) reported that avian predators selected males and small individuals of *M. townsendii* over females and large individuals. Small males were the most likely to be preyed upon, whereas large females were least likely. Boonstra (1977*a*) reported that, in tagged animals, neither sex nor weight class affected vulnerability to predation by avian predators. However, upon reanalyzing Boonstra's (1977*a*) data, Beacham (1979*a*) noted that males may have been selected more frequently by avian predators. Beacham (1979*a*) concluded that avian predation on *M. townsendii* was density dependent and, in contrast to Boonstra's (1977*a*) findings, he reported a 25% loss of *M. townsendii* to avian predators in a 1-week period.

In addition to the predators noted earlier, bobcats (*Felis rufus*), coyotes (*Canis latrans*), weasels (*Mustela* sp.), minks (*M. vison*), foxes (*Vulpes vulpes* and *Urocyon cinereoargenteus*), skunks (*Spilogale gracilis* and *Mephitis mephitis*), and snakes reportedly eat *M. townsendii* (Cowan and Guiguet, 1956; Maser and Storm, 1970; Maser et al., 1981).

Bayer (1981) found *M. townsendii* among the prey of great blue herons at a heron colony on Yaquina estuary in Oregon. He also observed herons to capture voles at William L. Finley National Wildlife Refuge, Oregon, but did not identify them to species. Taitt and Krebs (1983) reported that great blue herons could catch an average of three voles in an hour on Westham Island, British Columbia.

Giger (1965) found 31.9% of 2,886 skulls in regurgitated pellets of barn owls in Oregon in 1964 were those of *M. townsendii*. Monthly proportions of *M. townsendii* in the diet exhibited a distinct seasonal trend; they increased gradually from a low of 11.9% in May to a high of 76.3% in December, declined precipitously to 33.2% in January, then declined more gradually to 12.7% in April (Giger, 1965). Maser and Brodie (1966) did not distinguish among species of *Microtus* in regurgitated pellets of barn owls, long-eared owls (*Asio otus*), and great-horned owls, but listed *M. townsendii* among species represented.

Protection of *M. townsendii* from predation, especially by great blue herons, was accomplished by suspending fish netting over grassland, spreading straw for increased cover, or both (Taitt and Krebs, 1981, 1983). Taitt and Krebs (1983) also mowed a grassland area to reduce cover. From 2 February to 20 March 1981, protected populations had higher immigration, survival, and densities than unprotected populations. Voles in the mowed area suffered reduced survival. The highest density of voles was on an area with netting, extra cover, and extra food (Taitt and Krebs, 1983). From 20 March to 17 April, all populations, regardless of treatment, experienced reduced survival and densities. Taitt and Krebs (1983) concluded that the losses of voles during the first 6 weeks of the 1981 spring decline were the result of predation, but that losses during the last 4 weeks were the result of density-dependent dispersal.

Both Hilborn (1975) and Beacham (1979*d*) noted that identifiable families of *M. townsendii* tended to survive or disperse as a unit. When density increased or peaked, littermates tended to have similar life spans whether they dispersed or not, and littermates dispersed at about the same age (Beacham, 1979*d*). During cyclic peaks, adults and subadults dispersed during annual spring declines, and subadults and juveniles dispersed in summer and autumn (Beacham, 1979*c*). Beacham (1979*c*) found that voles born in spring dispersed before onset of breeding the following year, but autumn-born voles dispersed during the breeding season the following year. Dispersing voles <50 g had faster growth rates than residents of the same size; dispersing and resident voles in the 50- to 59-g weight class exhibited no consistent trend; and voles >59 g had slower growth rates when they dispersed than similar-sized residents (Beacham, 1979*c*).

Krebs et al. (1976) and Beacham (1981) found that sexual maturity was achieved at lower body mass in dispersers than in residents, but at least some subadults became reproductively mature before dispersal (Beacham, 1981). More males than females disperse (Beacham, 1981; Krebs et al., 1976). The number of voles that "disappeared" from five Townsend's vole populations during the month of onset of breeding in females was highly correlated with density of voles (Taitt and Krebs, 1983). Boonstra et al. (1987) reported that about twice as many females of *M. townsendii* and three other species of *Microtus* matured near their natal site. However, in enclosed populations similar proportions of males and females remained near the natal site at maturity suggesting that disruption of dispersal eliminated the tendency of more females to mature near the natal site than males. In each instance mature males moved about twice as far from natal sites as females (Boonstra et al., 1987).

Beacham (1980*d*) enclosed two populations of *M. townsendii*, but provided an area for dispersal inside each enclosure. He reported the percentage of loss by dispersal was correlated mainly with season; dispersal rates were lowest during winter nonbreeding periods and highest during spring declines in the peak year. Beacham (1980*d*) determined that there was no correlation between rate of population increase and dispersal rate. In contrast, Krebs et al. (1976) reported higher dispersal rates during population increases with faster growing populations having relatively more dispersal. In Beacham's (1980*d*) study high dispersal rates were concurrent with a moderately declining population. Hilborn and Krebs (1976) found no dispersal in *M. townsendii* during a moderate decline, but Krebs and Boonstra (1978) suggested that the results of Hilborn and Krebs (1976) may not be generally valid for *M. townsendii*.

Boonstra and Krebs (1977) prevented dispersal by fencing a high-density population of *M. townsendii*. The enclosed population increased to even higher densities, severely overgrazed the vegetation, and declined sharply. At least five other species of *Microtus* exhibited the "fence effect" (Lidicker, 1985). Dramatic increases in density in enclosed populations are considered the best evidence that *Microtus* populations sometimes are regulated by dispersal (Lidicker, 1985).

Large males usually have a survival advantage compared to smaller males, but large females are at a disadvantage compared to smaller females (Boonstra and Krebs, 1979). Boonstra and Krebs (1979) reported that rates of survival for males were related inversely to density and the rapidity of population increases, but that female survival was not related to density or growth rate of populations. Beacham (1980*d*) reported that female survival rates were moderately related to population growth rates and male survival rates were correlated closely with population growth rates. Large *M. townsendii* of both sexes had higher rates of survival than small ones during moderate spring declines, but during severe declines large and small females survived equally poorly (Beacham, 1980*c*). Survival rates of Townsend's voles are highest when population density is increasing and lowest during decreases (Beacham, 1980*b*). Survival in females is greater than in males (Beacham, 1979*b*, 1980*b*). Mortality is higher in postweanlings than in any other age class (Beacham, 1979*b*). Boonstra (1977*c*) found that more young *M. townsendii* survived during a spring decline on a grid on which the density of voles was maintained at a lower level than on a control grid. During light to moderate spring declines, most of the decrease in density of voles is caused by dispersal, but during severe declines most of the losses are attributable to death (Beacham, 1980*c*; Hilborn and Krebs, 1976). Males reportedly disappear more rapidly than females (Beacham, 1980*c*). Beacham (1980*d*) found no correlation between percentage of loss explained by dispersal and survival of males or females.

Home ranges of Townsend's voles based on a bivariate home-range model (Koeppl et al., 1975) and data collected in British Columbia (Taitt and Krebs, 1981) averaged about 900 m^2 for males and 500 m^2 for females (Madison, 1985). Addition of food to grids resulted in significantly smaller home ranges for both males and females (Taitt and Krebs, 1981; Taitt et al., 1981). Females on grids provisioned with extra food and males on grids with extra cover had the smallest home ranges (Taitt et al., 1981). Voles on grids to which extra food was added grew larger and a larger proportion attained breeding condition than on a control grid (Taitt and Krebs, 1981). Taitt and Krebs (1985) suggested that reduction in the size of home ranges of residents permitted immigrants to colonize new habitat in proportion to the amount of food available. When extra food is available, recruitment is biased toward females suggesting that females are the first to respond to the extra food (Taitt and Krebs, 1983).

Krebs et al. (1976) reported that if voles were removed from an area, new voles colonized it. The colonizers were more subordinate behaviorally than control residents, but established a breeding population if allowed to remain (Krebs et al., 1978). When a vole population is fenced, the enclosed habitat supports a much higher density than controls (Boonstra and Krebs, 1977), suggesting that food, space, and nests do not limit density of vole populations directly.

Taitt and Krebs (1985) identified four probable cycles in four populations and 13 annual fluctuations in three populations of *M. townsendii*. Cyclic peaks ranged from 525 to 800 voles/ha and averaged 697 voles/ha. Mean annual fluctuations ranged from 94 voles/ha to 239 voles/ha. Townsend's vole attains the highest average density of any North American *Microtus* (Taitt and Krebs, 1985). Annual fluctuations in density of *M. townsendii* populations are preceded by substantial spring declines, but during years of peak density the spring decline is slight (Taitt and Krebs, 1985). Both numbers of males and females decline in the spring of an annual fluctuation, but numbers of females do not decline in spring during a cyclic peak (Taitt and Krebs, 1985).

Pellets (Krebs et al., 1977) or silastic implants (Gipps et al., 1981) of testosterone in male *M. townsendii* had no significant effect on population dynamics, but silastic implants of scopolamine HBr reduced the rate of spring decline (Gipps, 1982; Gipps et al., 1981). When males were implanted with scopolamine HBr females in the population bred earlier and more females bred in the spring (Gipps et al., 1981). Males had higher rates of survival when females were fed mestranol, a synthetic steroid that renders females anestrous (Taitt and Krebs, 1982). Females with implants of testosterone had lower survival and larger home ranges than controls (Taitt and Krebs, 1982).

Taitt and Krebs (1981) suggested that annual fluctuations in density of *M. townsendii* in most years may result from cessation of reproduction in winter. They hypothesized that the rising water table during winter concentrates voles resulting in increased interaction, weight loss, and cessation of breeding. Body mass and female behavior seem to be factors influencing population fluctuations in Townsend's vole (Taitt and Krebs, 1985), and both appear to be affected by a combination of intrinsic and extrinsic factors. Space free from intruders may be a limiting factor for females, and the availability of breeding females the limiting factor for males (Krebs, 1984). Taitt and Krebs (1983) suggested that interactions of spacing behavior, predation, food availability, and availability of temporally suitable habitat may determine whether a population undergoes annual fluctuations or multiannual cycles.

To test the hypothesis that *Microtus* competitively excludes *Peromyscus maniculatus* from grasslands, Redfield et al. (1977) removed *Microtus* continuously from two areas south of Vancouver, British Columbia, for 2 years and disrupted the social organization of *Microtus* on another area for 2 years. On one removal grid, *M. townsendii* and *M. oregoni* occurred, but on the other *M. townsendii* was the only *Microtus* present. Densities of *Peromyscus* populations increased dramatically on grids from which *Microtus* was removed and on the grid where *Microtus* social organization was disrupted. On the control grid, density of the *Peromyscus* population remained extremely low. Male *Peromyscus* were 9% easier to trap and reproduction of *Peromyscus* appeared to start earlier in the year and extend later in autumn in the absence of *Microtus*. When Redfield et al. (1977) allowed *M. townsendii* to recolonize the grid, the number of *Peromyscus* declined rapidly. Results of their study support the conclusion that *Peromyscus* suffers from competition with *Microtus* in grasslands (Grant, 1971).

Microtus townsendii is among the most difficult voles to capture and census (Hilborn, 1982). Several weeks of prebaiting may be needed before *M. townsendii* will enter traps (Hilborn, 1982; Taitt and Krebs, 1985). Standard methods with Longworth or Sherman live traps generally do not result in capture of significant proportions of *M. townsendii* populations (Hilborn, 1982). Beacham (1982) reported live traps caught only 55% of a known *M. townsendii* population. Live traps are more likely to catch larger individuals (Beacham, 1982; Boonstra and Krebs, 1978); pitfall traps are more likely to catch smaller individuals. According to Beacham and Krebs (1980) live traps and pitfall traps sample different segments of the population with respect to size, wounding levels, and parasite loads. Use of both types of traps is necessary to sample different size and age classes in the population (Beacham, 1982; Beacham and Krebs, 1980; Boonstra and Krebs, 1978; Hilborn, 1982). Krebs and Boonstra (1984) recommended that the Jolly measure for ease of trapping (Jolly and Dickson, 1983) be used for comparisons between different population studies or trapping techniques. Townsend's vole enters traps occupied previously by conspecifics significantly more readily than they enter clean ones (Boonstra and Krebs, 1976). *Microtus townsendii* can be caught in snap traps set crosswise in runways and can be collected readily by hand under old boards, hay bales, and other similar sources of cover (Maser and Storm, 1970), and they can be captured by hand while fields are being plowed (MacFarlane, 1977).

Ectoparasites reported to infest *M. townsendii* include mites (Acari): (Glycyphagidae) *Glycyphagus hypudaei*; (Laelapidae) *Androlaelaps fahrenholzi*, *Echinonyssus isabellius*, *E. obsoletus*, *Eubrachylaelaps debilis*, *Eulaelaps stabularis* (Whitaker and Maser, 1984), *Haemogemasus occidentalis* (Keegan, 1951 [original description and type-host]; Whitaker and Maser, 1984), *H. reidii*, *Laelaps kochi*; (Listrophoridae) *Listrophorus mexicanus* (Whitaker and Maser, 1984); (Psorergatidae) *Psorergates townsendii* (Giesen et al., 1983 [original description and type-host]); (Trombiculidae) *Neotrombicula jewetti* (Brennan and Wharton, 1950; Easton, 1975; Wharton and Fuller, 1952); a louse (Anoplura): (Hoplopleuridae) *Hoplopleura acanthopus* (Spencer, 1966); a beetle (Coleoptera): (Leptinidae) *Leptinus occidentamericanus* (Peck, 1982 [original description]); flies (Diptera): (Cuterebridae) *Cuterebra grisea* (Beacham and Krebs, 1980; Boonstra, 1977*b*, Boonstra and Krebs, 1978; Boonstra et al., 1980); *Wohlfarhrtia vigil* (Boonstra, 1977*b*; Boonstra and Krebs, 1978); fleas (Siphonaptera): *Atyphloceras multidentatus* (Holland, 1949; Hopkins and Rothschild, 1962; Hubbard, 1947; Macchiavello, 1954), *Catallagia charlottensis* (Holland, 1949; Hopkins and Rothschild, 1962; Hubbard, 1947; Macchiavello, 1954; Svihla, 1941), *C. sculleni* (Hopkins and Rothschild, 1962), *Corrodsylla curvata* (Hubbard, 1947), *C. kohlsi* (Fox, 1940 [described as *Corypsylloides spinata*]; Macchaivello, 1954), *Delotelis hollandi* (Hopkins and Rothschild, 1962; Smit, 1952 [original description and type-host]), *D. telegoni* (Holland, 1949; Hubbard, 1947; Jellison and Senger, 1976; Macchiavello, 1954), *Epitedia scapani* (Hopkins and Rothschild, 1962; Hubbard, 1947; Macchiavello, 1954), *Hystrichopsylla dippiei* (Hubbard, 1947; Macchiavello, 1954; Svihla, 1941), *H. occidentalis* (Holland, 1957; Hopkins and Rothschild, 1962), *Megabothis abantis* (Hubbard, 1947; Macchiavello, 1954; Svihla, 1941; Wagner, 1936), *Megabothris quirini* (Hubbard, 1947), *Monopsyllus wagneri* (Hubbard, 1947; Macchiavello, 1954), *Opisodasys keeni* (Holland, 1949; Macchaivello, 1954), *P. selenis* (Hopkins and Rothschild, 1971; Svihla, 1941), *Rhadinopsylla sectilis* (Hopkins and Rothschild, 1962; Hubbard, 1941, 1947 [reported as *Micropsylla goodi*]; Macchiavello, 1954); a tick (Acari): (Ixodidae) *Ixodes angustus* (Bishopp and Trembley, 1945; Cooley and Kohls, 1945; Easton and Goulding, 1974). Easton and Goulding (1974) reported nymphs and adult males of the tick *Ixodes angustus* in nesting material of *M. townsendii*, but did not describe the criteria by which the nests were distinguished from those of other small-mammal species in the area.

Boonstra (1977*b*) found 5.4% of 1,933 *M. townsendii* captured at Westham Island, British Columbia, parasitized by the grey flesh fly (*Wohlfahrtia vigil*). He suggested presence of botfly larvae may increase the chances of parasitism by *W. vigil*. All age classes of voles seemingly were equally susceptible. Only 5% of those parasitized by *W. vigil* were alive 2 weeks later, a survival rate 13.2 times lower than in a control population (Boonstra, 1977*b*). The earliest date of parasitism by the flesh fly was 12 June with all other infestations occurring between 22 July and 14 October. The period of maximum infestation was August and early September.

BEHAVIOR. Townsend's vole is active throughout the year and appears to be active both day and night (Bailey, 1936; Dalquest, 1948; Maser and Storm, 1970). It is a good swimmer and diver (Maser et al., 1981), and readily enters water; it is able to swim across small streams. Townsend's vole has been captured even in traps set underwater (Elliot, 1903).

According to Krebs et al. (1978) dispersing *M. townsendii* showed less wounding, was more submissive in staged encounters, and vocalized more than nondispersing voles. Anderson (1975) reported zero heritability for agonistic behavior in *M. townsendii.* Lidicker (1985) suspected that dispersing *Microtus* is nonaggressive because it is not a resident and, upon reestablishing a home range, it becomes more aggressive. Krebs (1984) found no significant correlation between four agonistic behaviors of breeding *M. townsendii* and body weight for males or females. He found significant differences in behaviors between sexes, and between breeders and nonbreeders.

Krebs (1984) removed individuals of *M. townsendii* from a number of different field populations and performed agonistic bouts on 2,714 of them and activity tests on 1,270 of them. He was able to predict 13 of 14 demographic variables of the field populations from data obtained from standard laboratory bouts. Eleven of the variables were predicted from "aggressiveness" scores alone. Only five of the 14 variables were correlated with the activity data. One of the behavioral correlates was that the intensity of a spring decline was more severe when both male defensive scores and female aggressiveness scores were high (Krebs, 1984). Taitt and Krebs (1983) reported that male *M. townsendii* moved more during the breeding season and had more wounds than earlier in the spring. Females moved less while lactating than earlier in the spring.

Subadult males weighing 20 to 44 g and implanted with capsules containing testosterone fought more and investigated each other less than control males with dummy implants (Gipps, 1982). However, they fought less than adult control males >45 g. Adult males >45 g with implants containing scopalamine HBr fought significantly less than control males (Gipps, 1982). Females implanted with testosterone exhibited higher levels of wounding than untreated females and males (Taitt and Krebs, 1982).

In staged contests in which a winner could be determined, *M. oregoni* and *M. canicaudus* males dominated *M. townsendii* males (Weil, 1975). Weil (1975) found *M. townsendii* and *M. oregoni* more gregarious than *M. canicaudus* and noted that males of all three species displayed more solitary behavioral patterns than females. Mutual avoidance was more frequent when *M. townsendii* was involved in encounters. Pearson (1972) also noted that *M. townsendii* was more gregarious than *M. canicaudus*, but suggested that *M. townsendii* may be dominant over *M. canicaudus* where they occur together. Hawes (1975) suggested that *M. townsendii* competes with *M. oregoni* by interference competition, and *M. oregoni* appears to escape this interference by burrowing. When he introduced *M. townsendii* into an area previously occupied only by *M. oregoni*, both the population size of *M. oregoni* and the range of habitats used were reduced (Hawes, 1975).

Hip glands in *M. townsendii* reportedly are used in scent marking; marking action seems to consist of distinct figure-eight motions of the hips (MacIsaac, 1977). MacIsaac (1977) observed that a substantial amount of wounding that occurred during the reproductive season is concentrated in the vicinity of the hip glands.

GENETICS. Townsend's vole has a diploid chromosome number of 50; the entire complement is acrocentric (Hsu and Benirschke, 1971). The chromosomes grade in size from large to small without a significant break, thus, matching homologous pairs is difficult. The X chromosome is one of the larger elements, the Y one of the smaller (Hsu and Benirschke, 1971).

LeDuc and Krebs (1975) monitored gene frequency at the leucine aminopeptidase (LAP) locus in a population of *M. townsendii* and reported a positive association between changes in the LAP-F allele and changes in population density. However, experimental manipulation of LAP genotypes failed to produce alteration in overall population dynamics (LeDuc and Krebs, 1975). Krebs et al. (1976) reported a trend of increased population density associated with increases in LAP-F frequency. Anderson and Boonstra (1979) concluded that litter size at recruitment was unrelated to the LAP genotype of the mother or the loss of entire litters.

Anderson (1975) attempted to examine heritability of some quantitative traits in *M. townsendii* by releasing full siblings into natural populations. The heritability (±*SE*) of six traits is as follow: dispersal tendency (0.62 ± 0.11), duration of life (0.37 ± 0.08), adult agonistic behavior (0.00), juvenile growth rate (0.46 ± 0.24), maximum body mass (0.00), and age at sexual maturity (0.55 ± 0.20).

Thomas and Beckenbach (1986) divided individuals of *M. townsendii* collected from seven different localities into seven maternal lines based on restriction enzyme analysis of mitochondrial DNA (mtDNA). Samples from Vancouver Island, British Columbia, were separated into two major maternal lines with a divergence of 0.453 ± 0.240%. The insular lines were 0.677 ± 0.257% divergent from the most closely related mainland population, suggesting that the voles on Vancouver Island were not derived from recent colonizations from the mainland. In contrast, Thomas and Beckenbach (1986) found no detectable variation within Townsend's vole population on Bowen Island, British Columbia, or divergence from an adjacent mainland population, indicating a recent colonization. The Townsend's vole mtDNA is 16,400 ± 500 base pairs; gene order appears to be conserved in comparison to laboratory mouse mtDNA (Thomas and Beckenbach, 1986).

REMARKS. The generic name *Microtus* is from the Greek *mikros* meaning "small" and *otos* meaning "ear" (Jaeger, 1955); the specific name *townsendii* refers to John Kirk Townsend, who collected the type specimen (Bachman, 1839) in 1835.

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